

THE AFFINITIES OF LIASSIC AND LATER ICHTHYOSAURS

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ABSTRACT. Ichthyosaurs from low in the Hettangian of Britain, with fore limbs showing a mixture of longipinnate and latipinnate characters, differing vertebral column functions, and differing hind-limb proportions, suggest that latipinnates evolved from Hettangian or late Triassic longipinnates and not from the Middle Triassic mixosaurs as has long been held. The latter are removed from ancestry of Liassic and later latipinnates on the grounds of their earlier and short stratigraphical range, their more advanced morphology, and because a comparison of the trends in mixosaurs and in Liassic and later latipinnates shows that these are often divergent. *Ichthyosaurus intermedius* and *I. communis* are restored as separate species, and the following new taxa are erected: Order Longipinnatoidea, Order Latipinnatoidea, Order Heteropinnatoidea, and Order Mixosauroida. Two new families, the Protoichthyosauriidae and the Leptopterygiidae, are defined and referred to the heteropinnatoids. The new genus *Protoichthyosaurus* and its two species *Protoichthyosaurus prostaialis* sp. nov. and *P. prosotaialis* sp. nov. are described. *Leptopterygius tenuirostris* presents particular taxonomic difficulties since it is an indivisible species showing every gradation of structure between longipinnatoid and heteropinnatoid individuals.

THE ichthyosaurs were largely oceanic, dolphin-like reptiles with highly adapted limbs, a long snout, posteriorly placed nasal openings, and a vertical propulsive tail. Their general anatomy and mode of life were known by the end of the nineteenth century and an origin of Liassic ichthyosaurs in *Mixosaurus* Baur was suggested by Fraas in 1891, a theory which has persisted. It has also long been held that ichthyosaurs can be divided into two groups—latipinnates and longipinnates—based largely upon the differing structure of their fore limbs (Kiprijanoff 1881; Lydekker 1889; von Huene 1922). McGowan (1972) sought to confirm this by using certain cranial features in addition to fore-limb structure, and reasserted that the mixosaur stock with its more primitive pentadactyl limb gave rise to the later latipinnate ichthyosaurs.

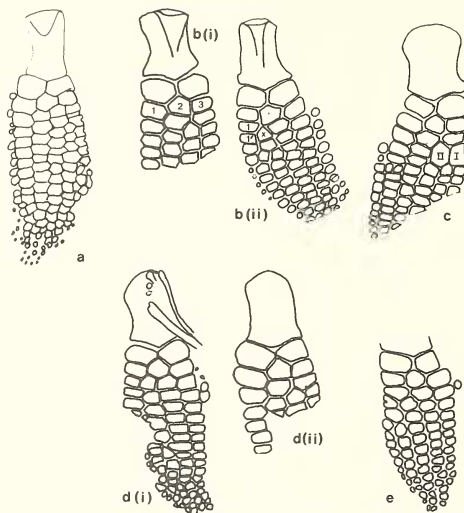
It is the purpose of this paper to show, in the light of new mixosaurian materials and a fresh examination of mixosaurs as a whole both morphologically and temporally, that mixosaurs had no direct descendants, and that certain ichthyosaurs from very low in the Liassic show a variety of conditions intermediate between those of latipinnates and longipinnates, thus suggesting that latipinnates arose from longipinnates.

Abbreviations. B. Museum and Library, Queen Square, Bath; BCM, Bristol City Museum; BMNH, British Museum (Natural History); CJS, Messrs. C. J. Clark & Co., Street, Somerset; LM, Leicester Museums, Art Galleries and Record Service; MMNH, Museum of Natural History, Milan; NM, Newark Museum; NMA, Northampton Museum and Art Gallery; NMW, National Museum of Wales; OUM, Oxford University Museum; UPMZ, University Palaeontological Institute and Museum, Zurich; US and RIS, University College and the Royal Institution, Swansea.

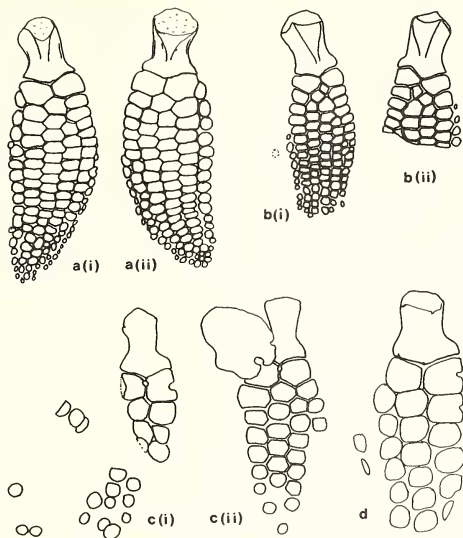
'Composite forms' McGowan (1972) gave a number of criteria by which he considered that longipinnate and latipinnate ichthyosaurs could be distinguished. For example, the fore limbs of longipinnates had three primary digits and distal

carpals, and the intermedium supported only one digit; finger-splitting probably did not occur, and the radius was probably notched. In the latipinnate fore limb, McGowan believed, there were four primary digits and distal carpals, and the intermedium supported two digits; finger-splitting usually occurred, and the radius was rarely notched.

Over the last few years unusual ichthyosaur fore-limbs from the Lower Jurassic of Britain have been studied, including that figured by McGowan (1969, 1974) which, using his (1972) criteria, cannot be termed either latipinnate (text-fig. 1*a*) or



TEXT-FIG. 1. Ichthyosaur fore limbs. (Over-all length of humeri given in cm.) *a*, *Ichthyosaurus intermedius* Conybeare BMNH 2013. Lower Liassic, Street, Somerset. Right fore limb, ventral view (9.8 cm); *b* (i), (ii), *Protoichthyosaurus prostaxalis* gen. et sp. nov. B. 1963'5/O.S., Moore Collection. Almost certainly Lower Liassic, Street, Somerset. (i), left fore limb, ventral view (6.6 cm); (ii), right fore limb, ventral view (7.0 cm); *c*, *P. prostaxalis* gen. et sp. nov. B. 1963'7/O.S., Moore Collection. Almost certainly Lower Liassic, Street, Somerset. Left fore limb, ventral view (7.1 cm); *d* (i), (ii), *P. prostaxalis* gen. et sp. nov. B. 1963'15/O.S., Moore Collection. Almost certainly Lower Liassic, Street, Somerset. (i), left fore limb, dorsal view (9.5 cm); (ii), right fore limb, dorsal view (9.15 cm); *e*, *P. prostaxalis* gen. et sp. nov. LM 454'1951/164, Faulkes Collection. Lower Liassic, Leicestershire. Split slab (length excluding humerus 13.7 cm).



TEXT-FIG. 2. Ichthyosaur fore limbs. (Over-all length of humeri given in cm.) *a* (i), (ii), *Protoichthyosaurus prostaxialis* gen. et sp. nov. OUM J13,799, Duke of Marlborough's Collection. Lower Liassic, Street, Somerset. (i), left fore limb, ventral view (7.1 cm); (ii), right fore limb, ventral view (7.3 cm); *b* (i), (ii), *P. prosostealis* gen. et sp. nov. B. 1963/24/O.S., Moore Collection. Almost certainly Lower Liassic, Street, Somerset. (i), left limb, ventral view (10.95 cm); (ii), right limb, ventral view (9.5 cm); *c* (i), (ii), *Leptopterygius tenuirostris* (Conybeare) B. 1963/8/O.S., Moore Collection. Lower Liassic, Street, Somerset. (i), left fore limb, ventral view; (ii), right fore limb, ventral view (9.4 cm); *d*, *Leptopterygius* sp. B. 1963/17/O.S. Moore Collection. Lower Liassic, almost certainly from Street, Somerset. Right fore limb (10.7 cm).

longipinnate (text-fig. 2*d*). They can be divided into three groups, which are designated here as 'composite' forms.

Group 1. These specimens usually have one typically latipinnate fore limb and one characterized by two transverse carpal rows, each comprising three bones from which four digits arise, as though becoming latipinnate one transverse row more distal than usual (text-figs. 1*b* (i), 1*c*, 1*d* (ii), 1*e*, and 2*a* (i). The extra digit appears to originate on the radial side (text-fig. 1*c*, bones I and II). In the most longipinnate-like form, the first radial phalanx is notched (text-fig. 1*e*).

The bone marked 'X' in text-fig. 1*b* (ii) has an extremely small contact with the intermedium. The limb is therefore only just latipinnate.

Group 2. Only one specimen of this group is known (text-fig. 2*b* (i), (ii)). Both fore limbs possess an extra diamond-shaped bone surrounded by the radius, radiale, anterior centrale, intermedium, and ulna. The anterior centrale borders only a small part of this element in the right limb and virtually none in the left. Finger-splitting occurs on the radial side in the fifth transverse phalangeal row in both limbs, and in the eighth row of the more complete left limb; there is also distal uniting of fingers in the radial digit at the eleventh row.

Group 3. The specimen illustrated is *Leptopterygius tenuirostris* Conybeare. It is longipinnate except that it possesses a fourth distal carpal and finger, which arises on the ulnar side of the limb (text-fig. 2*c* (ii)). The notched radius (text-fig. 2*c* (i)) is typical of the species.

Complete ichthyosaurs with 'composite' fore limbs are rare, so it is difficult to assess the individuals in terms of McGowan's (1972) criteria. However, B. 1963' 7/O.S. (text-fig. 1*c*) when examined in terms of orbital diameter divided by jaw length, gives a figure of 0.20, which places it on McGowan's longipinnate scale (McGowan 1972, Table 1). The length from the tip of the snout to the anterior tip of the maxilla, divided by the jaw length, gives a ratio of 0.42, which places it midway between Lower Liassic latipinnates and longipinnates, if the aberrant *Ichthyosaurus breviceps* is ignored. On the other hand, the coracoid is clearly latipinnate, suggesting that 'composite' characters extend to other parts of the body. Clearly these specimens cannot be allocated using McGowan's criteria which, although probably valid for the later forms (Appleby, in preparation), are unreliable for forms such as these from the earliest Liassic.

Turning to evidence for Triassic ancestry of the Lower Liassic forms (McGowan 1972), it should be noted that only one cranial value, the diameter of the orbit divided by the jaw length, is given for one species of *Mixosaurus*, which is allocated to the latipinnates only on the basis of its high value identical to that of the short-snouted aberrant *I. breviceps* and on its limb structure (McGowan 1972, Table 1). I agree with von Huene (1956), Romer (1966), and McGowan (1972) that the mixosaurs possessed a primitive tetrapod limb from which the Lower Jurassic latipinnates may have been derived, but many rearrangements have to be imagined between the two, for which no fossil evidence is known.

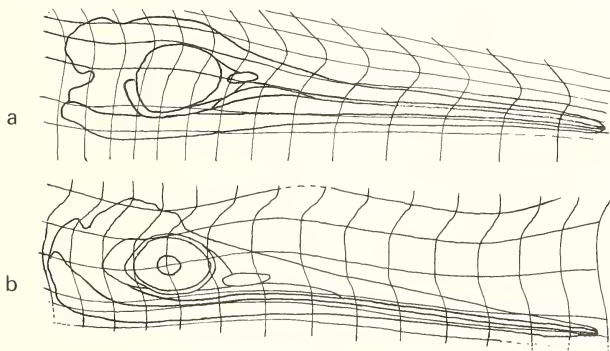
With doubts raised not only by the lack of a continuous lineage from mixosaurs to Lower Jurassic latipinnates, but also by the unexpected presence of 'composite' individuals at such a supposedly late evolutionary stage, this paper re-examines the relationship.

MIXOSAURS AND THE LOWER LIASSIC AND LATER LATIPINNATE ICHTHYOSAURS

Materials used. Photographs and specimens of sixteen mixosaurs from Europe, Spitzbergen, China, and North America, including new material kindly made available by Dr. Emil Kuhn-Schwyder, and thirty-eight Lower Jurassic and later latipinnates, mainly from Britain, are used in this part of the study. Some specimens are incomplete but provide statistical and/or morphological information. The Family Ophthalmosauridae is retained in the sense of Appleby (1956).

Stenopterygius quadricissus has been discussed by McGowan (1976) and allocated to the latipinnates. This seems inappropriate for, on any definition of the longipinnate fore limb, *S. quadricissus* is a classical longipinnate. The nasal opening and the coracoids are also typically longipinnate. McGowan has relied on phenetic affinity and cluster diagrams, a method which has been criticized generally by Appleby and Jones (1976). Similarities at the level of correlation stated do show up between the different species and genera used, but time sequences cannot be omitted when constructing a classification reflecting phylogeny, and McGowan was right when he observed that Upper Liassic longipinnates had advanced to a position which had been reached earlier by Lower Liassic latipinnates.

In order to confirm the taxonomic position of *Stenopterygius*, a typical latipinnate (*Ichthyosaurus* Conybeare, after McGowan 1974, fig. 2b, BMNH 39492) and a typical longipinnate (*Tenmodontosaurus* Lydekker, after von Huene 1922, pl. 3, fig. 3) were both matched to *Stenopterygius* using the AVR (Analogue Video Reshaper) (Appleby and Jones 1976) (text-fig. 3). More grid modification was required to match *Ichthyosaurus* to *Stenopterygius* than *Tenmodontosaurus* to *Stenopterygius* (cf. text-fig. 3a, b). For example, the height of the posterior part of the head and the upper jaw depth of *Tenmodontosaurus* are closer to those of *Stenopterygius*, and streamlining is also closer. This shows up particularly well in the non-linear stretch shown by the grid, which must be applied to the image of *Ichthyosaurus* to match it to *Stenopterygius*, a stretch which is absent in *Tenmodontosaurus*. The AVR results from the skulls of these three genera thus support the evidence cited above. Consequently *Stenopterygius* is retained in the longipinnates and is not used in this study.



TEXT-FIG. 3. Drawings made from AVR comparisons of *Ichthyosaurus* and *Tenmodontosaurus* with *Stenopterygius*. a, *Ichthyosaurus* Conybeare BMNH 39492, after McGowan (1974, fig. 2b). Lower Liassic, Lyme Regis, Dorset (reversed), matched to *Stenopterygius*, after von Huene (1922, pl. 10, fig. 3a); b, *Tenmodontosaurus* Lydekker, after von Huene (1922, pl. 3, fig. 3), matched to *Stenopterygius*. Original length of skulls: *Ichthyosaurus* (approx. 50 cm);

Stenopterygius (approx. 94 cm); *Tenmodontosaurus* (approx. 171.5 cm).

Stratigraphical distribution. With the exception of Appleby (1967) and McGowan (1972) and the possible, but improbable exception of Dechaseaux *in* Piveteau (1955) where the French is ambiguous, all authorities (including Merriam (1908), Wiman (1916), von Huene (1922, 1956), Appleby (1961), Kuhn-Schnyder (1964), Buchan *et al.* (1965), Young (1965) and personal communications (1976) with Professor Dr. E. Kuhn-Schnyder, Dr. H. Rieber, and Dr. G. Pinna) confirm that mixosaurs are restricted to the Middle Triassic. They are first known in various parts of the world from the earliest Anisian, and apparently became extinct at the end of the Anisian or, in Europe, at the very beginning of the Ladinian. The earliest latipinnate ichthyosaurs made their appearance in the Hettangian. There is, therefore, a large world-wide stratigraphical gap comprising most of the Ladinian, the Carnian, the Norian, and the Rhaetian, between the last-known mixosaur and the first-known latipinnate ichthyosaur.

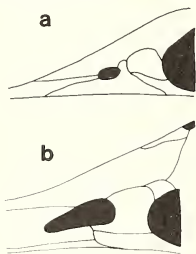
SOME MIXOSAUR ADVANCES NOT POSSESSED BY LOWER JURASSIC AND LATER LATIPINNATES

It is not intended to describe the mixosaurs in detail. Several descriptions already exist: Quenstedt 1852 (type description of *Mixosaurus atavus*); Hulke 1873 (type description of *M. nordenskiöldii*); Bassani 1886 (type description of *M. cornalianus*); Repossi 1902; Merriam 1910 (type description of *Phalarodon fraasi*); Wiman 1910, 1912, 1916; von Huene 1916, 1922, 1925; Edinger 1934; von Huene 1949; Kuhn-Schnyder 1964; Young 1965; Pinna 1967 (description of neotype of *M. cornalianus* (Bassani)); and Young and Dong 1972.

Further studies are being carried out by Professor Dr. Emil Kuhn-Schnyder and his colleagues. Below, a number of advanced features possessed by mixosaurs are described and contrasted with similar Lower Liassic and later latipinnate features. They include cranial features and features of the vertebral column, pectoral and pelvic girdles, and limbs. Trends are described where possible.

Cranial features

a. Maxilla (text-fig. 4). Dechaseaux (1955) observed that the maxillae of mixosaurs (text-fig. 4a) have dorsally directed processes which intervene between the nasal opening and the lacrymal to exclude the latter from taking part in the nasal opening,



TEXT-FIG. 4. Lachrymal regions of *Mixosaurus* and *Ichthyosaurus*. *a*, *Mixosaurus*, after Dechaseaux (1955). Late Anisian, Switzerland; *b*, *Ichthyosaurus* Conybeare, after Dechaseaux *in* Piveteau (1955). Lower Liassic, NW. Europe.

an observation supported by new material. Primitive tetrapods (*Hylonomus*, *Diadectes*, *Seymouria*, *Captorhinus*) possess a lachrymal which takes part in both orbital and nasal openings, and this primitive condition is retained in *Ichthyosaurus* from the lowest Jurassic and its later descendants (text-fig. 4b).

b. Palate. Compared with Lower Jurassic and later latipinnates, the interpterygoid vacuities in mixosaurs are narrow and substantially filled by the parasphenoid rostrum. Whereas the width between the lateral margins of the vacuities in *Ichthyosaurus* (Sollas 1916) and *Baptanodon* (Gilmore 1905) occupy one-third of the width of the palate, the same feature in *M. cornalianus* (von Huene 1916) occupies only one fourteenth, and the posterior end of the vacuity in *M. atavus* (von Huene 1916) is occupied by a broad triangular parasphenoid rostrum which is very narrow in later forms such as *Ichthyosaurus* and *Ophthalmosaurus*. The interpterygoid vacuities are open in primitive tetrapods, therefore the mixosaurs show an advance towards a more closed palate while the Lower Jurassic and later latipinnates retained the primitive condition (Appleby 1961).

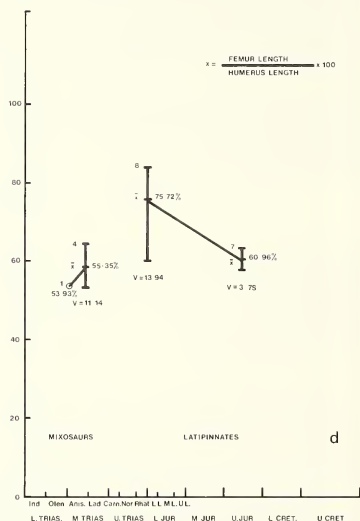
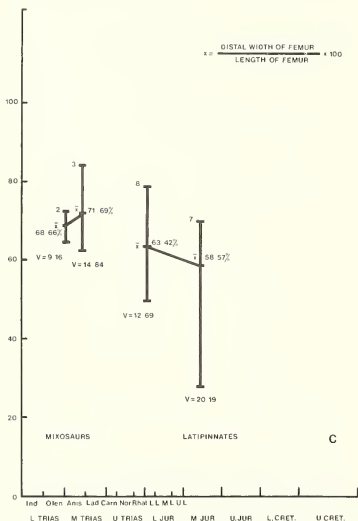
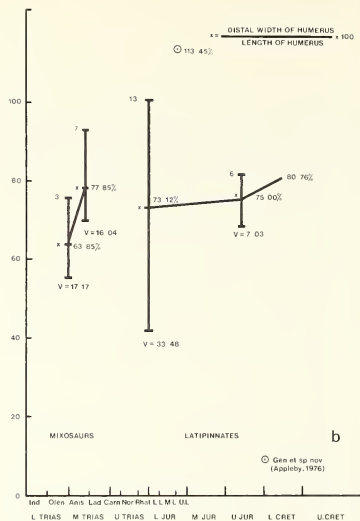
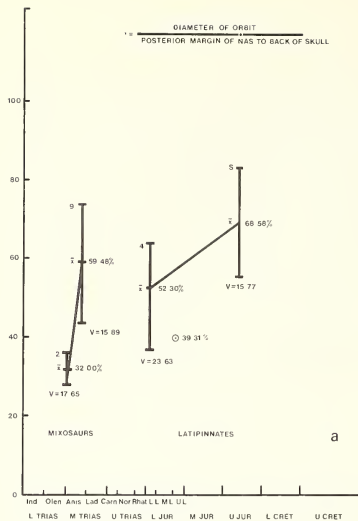
c. Orbits. McGowan (1972) does not give trends within mixosaurs in his consideration of the orbital diameters, but with more material available, and using the ratio of the diameter of the orbit divided by skull length from the posterior margin of the nasal opening to the posterior margin of the skull, for reasons given in Appleby (1961), the mean value of two early Anisian mixosaurs is 32% while the mean value of nine late Anisian/early Ladinian mixosaurs is 59.48%. The trend shows rapid increase in mean relative size of the orbit. See Table 1 and text-fig. 5a.

The symbols used in all the tables are in accordance with Simpson, Roe, and Lewontin (1960). O.R. = observed range of the variate; \bar{X} = the sample mean followed by the confidence interval for the mean (at the 95% level); N = number of individuals in the sample; S = standard deviation of the sample, and V = coefficient of variation.

TABLE 1. $X = \frac{\text{Diameter of orbit}}{\text{Skull length posterior to nasal opening}} \%$

	O.R.	\bar{X}	N	S	V
Early Anisian mixosaurs	28.00-36.00	32.00 \pm 50.77	2	5.65	17.65
Late Anisian/early Ladinian mixosaurs	43.22-73.52	59.48 \pm 7.26	9	9.45	15.89
All mixosaurs	28.00-73.52	54.48 \pm 9.57	11	14.25	20.19
Lower Liassic latipinnates	36.50-63.60	52.30 \pm 19.66	4	12.36	23.63
Upper Liassic latipinnate	39.31	39.31	1	—	—
Upper Jurassic latipinnates	55.23-85.22	68.58 \pm 13.43	5	10.82	15.77

The trend also shows a rapid increase in the total range of variation in mixosaurs. Using the same procedure with the Lower Jurassic and later latipinnates, results obtained show an increase in the diameter of the orbit from the Lower to the Upper Jurassic. The mean value for the four specimens from the Lower Jurassic (two *Ichthyosaurus communis*, one *I. breviceps*, and one *I. intermedius*—the latter believed to be synonymous with *I. communis* by McGowan 1972, 1974) is 52.30%, rising to 68.58% for five ophthalmosaurid species drawn from *Ophthalmosaurus* and *Baptanodon* (Gilmore 1905; Andrews 1910; Appleby 1958) from the Upper Jurassic of England and North America respectively (Table 1 and text-fig. 5a). The increase in



TEXT-FIG. 5. Quantitative comparisons of early and late mixosaurs with Liassic and late Jurassic and/or Cretaceous latipinnates. *a*, diameter of orbit expressed as percentage of length from posterior margin of nasal opening to back of skull; *b*, distal width of humerus expressed as percentage of length of humerus; *c*, distal width of femur expressed as percentage of length of femur; *d*, length of femur expressed as percentage of length of humerus.



TEXT-FIG. 6. *Mioxosaurus nordenskiöldii* (Hulke) BMNH 5701. Middle Triassic, probably Anisian, Edge Island, Spitzbergen.



TEXT-FIG. 7. *Mioxosaurus* sp. UPIMZ EK-S/RMA 4-1976. Upper Anisian, Monte San Giorgio, Tessin, Switzerland (approx. 80 cm long).

the diameter of the orbit shown here is not as steep as that shown by the mixosaurs which had, in general, reached a more advanced state at extinction than the latipinnate ichthyosaurs at their first appearance.

McGowan's (1972) single mixosaur orbital value also shows a mixosaur advance over all the Lower Liassic latipinnate ichthyosaurs listed, with the exception of *I. breviceps* whose short jaw raises the ratio for this species and distorts McGowan's trends.

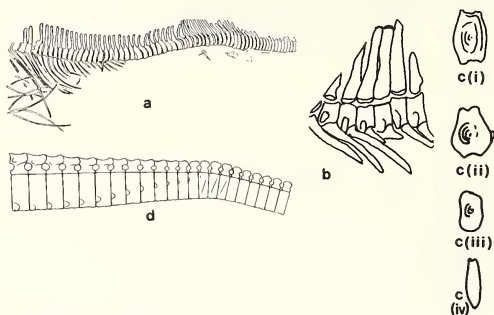
Vertebral column

The vertebral columns of both mixosaurs and Lower Jurassic and later latipinnates are advanced over the primitive condition, but in divergent directions.

In mixosaurs the neural spines are very high along the whole length of the vertebral column (text-figs. 6 and 7 and Dechaseaux 1955), but in the caudal region posterior to the shortening of the ribs, they rise even higher from approximately twice to three times the height of the centrum, then fall away rapidly towards the tip of the tail (text-fig. 8*a, b*). The spines are inclined posteriorly at the anterior end of the caudal rise, and anteriorly at the posterior end. In the region of the highest spines, the rib facets are low on the sides of the centra. The posteriormost centra are laterally

compressed (von Huene 1916) (text-fig. 8c (iv)) unlike the more anterior centra (text-fig. 8c (i), (ii), and (iii)).

The Lower Jurassic and later latipinnate ichthyosaurs show different advances. The neural spines are reduced in height and become effectively ball-and-socket joints formed by the zygapophyses in the caudal region. There is a sharp downward bend in the tail comprising approximately three wedge-shaped centra (text-fig. 8d), and the



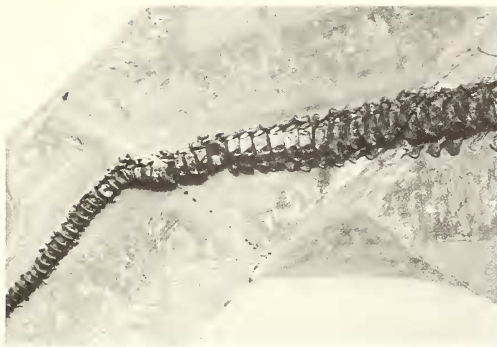
TEXT-FIG. 8. Vertebral column bones of ichthyosaurs. *a*, *Mixosaurus nordenskiöldii* (Hulke), after Wiman (1910). Lowest Anisian, Spitzbergen; *b*, *M. natans* Merriam, after Merriam (1908). Anisian, Nevada; *c* (i), (ii), (iii), mixosaur centra from anterior to posterior caudal, after von Huene (1916). *c* (i), *M. atavus*, Palmberg; *c* (ii), *M. atavus*, Althengstätt; *c* (iii), *M. atavus*, Röthenbach; *c* (iv), *M. cornalianus*, after Repossi (1902). Lombardy, Italy; *d*, schematic drawing of part of caudal region of *Ichthyosaurus*. Lower Liassic.

rib facets rise from a low position in the pelvic region to the dorsolateral margin of the centrum at the tail-bend (text-fig. 9). However, the centra posterior to the tail-bend are laterally compressed as in mixosaurs and are without rib facets. The functions of such differing structures are discussed below.

Pectoral girdle

The chief advance in the mixosaur pectoral girdle is the change in the type of coracoid found in the early Anisian, which have almost parallel median and lateral margins (text-fig. 10a), to the type found in the late Anisian/Ladinian, which have antero-mesially rounded margins (text-fig. 10b). At the same time, the interclavicle evolved from a straight-edged triangle to a waisted tri-radiate shape. The clavicle and scapula remained virtually unchanged.

Lower Jurassic and later latipinnates have very different pectoral girdles. At their inception in the Hettangian, the glenoid articulation of the mesially rounded coracoid was more anteriorly placed (text-fig. 10c) and there were distinct anterior and posterior notches, while the scapula was much broader proximally than distally—

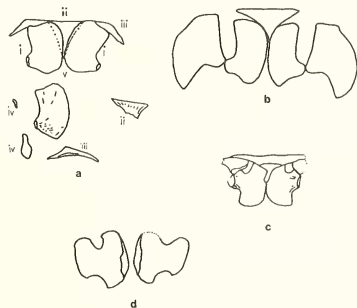


TEXT-FIG. 9. Detail of the caudal region at the tail-bend of *Ichthyosaurus intermedius* Conybeare BMNH 2013. Lower Liassic, Street, Somerset (approx. 30 cm long).

unlike the mixosaur scapula which is axe-head shaped—and had a hollow for the scapulo-humeralis anterior musculature. The dermal girdle is more lightly built with a T-shaped interclavicle (text-fig. 10c). Text-fig. 10d shows the condition in *Ophthalmosaurus icenicus*.

Pectoral limb

The mixosaur fore limb as a whole shows no obvious advances of general structure over that of the Lower Jurassic and later latipinnates, but the proportions of the mixosaur humerus show trends which suggest that the evolution of this element was more rapid and reached a more advanced stage than that of the later forms from low in the Lower Jurassic.



TEXT-FIG. 10. Ichthyosaur pectoral girdles. *a* (i), (ii), (iii), (iv), (v), *Mixosaurus maotaiensis* Young. Early Anisian, Kweichow, China. (i), coracoid; (ii), interclavicle; (iii), clavicle; (iv), ?parts of scapula; (v), my restoration of girdle excluding scapula (all after Young (1965)); *b*, *M. cornalianus* (Bassani), after Wiman (1912). Late Anisian/early Ladinian. Pectoral girdle lacking clavicles; *c*, *I. intermedius* Conybeare, after von Huene (1922). Lower Liassic, Watchet, Somerset. Almost entire pectoral girdle; *d*, *Ophthalmosaurus icenicus* Seeley, after Appleby (1956). Oxford Clay, Peterborough. Left and right coracoids.

The distal breadth of the humerus, expressed as a percentage of its length, may be used as a guide to the foreshortening of the limb. The early Anisian mean for mixosaurs is 63.85%, while late Anisian/Ladinian forms have a value of 77.85%. The range of variation is also higher in late Anisian/Ladinian forms (text-fig. 5b, Table 2).

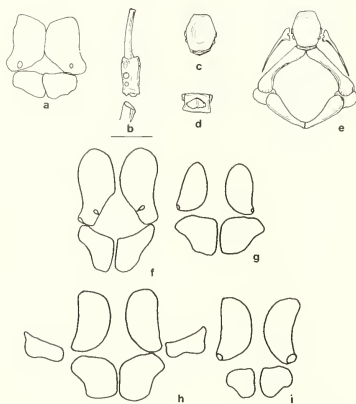
TABLE 2. $X = \frac{\text{Distal width of humerus \%}}{\text{Length of humerus \%}}$

	O.R.	\bar{X}	N	S	V
Early Anisian mixosaurs	56.17-77.77	63.85 \pm 27.25	3	10.97	17.17
Late Anisian/Early Ladinian mixosaurs	69.84-92.85	77.85 \pm 11.55	7	12.49	16.04
Lower Liassic latipinnates	41.62-100.00	73.12 \pm 14.78	13	24.46	33.45
Upper Liassic latipinnate	113.45	113.45	1	—	—
Upper Jurassic latipinnates	68.42-81.25	75.00 \pm 6.08	6	5.29	7.03
Cretaceous latipinnate	80.76	80.76	1	—	—

In contrast, the rate of foreshortening of the humerus in Lower Jurassic and later latipinnates was much slower. The Lower Liassic mean is 73.12%. Only one Upper Liassic species of latipinnate is known (Appleby: in preparation) and its value in contrast is 113.45%. Upper Jurassic latipinnates have a slightly higher mean of 75.00% but the range of variation is much reduced. The single Lower Cretaceous latipinnate *Myobradypterygius hauthali*—an obviously latipinnate form (text-fig. 14g)—has a value of 80.76%.

Pelvic girdle

The pelvic girdle in mixosaurs shows three main advances between the earliest Anisian and the late Anisian/Ladinian boundary: an over-all decrease in the girdle (text-fig. 11a, g), a decrease in the relative size of the pubis (text-fig. 11a, i), and the

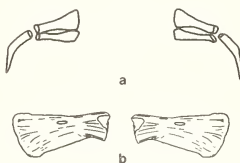


TEXT-FIG. 11. Mixosaur pelvic girdles brought to approximately the same width at the ischiadic portion of the acetabulum. *a-e*, *Mixosaurus nordenskiöldii* (Hulke), after Wiman (1910). Earliest Anisian, Spitzbergen. *a*, ischia and pubes, dorsal view; *b*, sacral vertebra and proximal end of ilium, lateral view; *c*, vertebral centrum, end view; *d*, the same, ventral view; *e*, reconstruction of girdle and sacral vertebra with ribs, posterior view; *f*, *M. atavus* (Quenstedt), after von Huene (1916). Early Anisian, Palmberg and Rohrdorf. Ischia and pubes; *g*, *Mixosaurus* sp. UPMIZ EKS/RMA 6-1976. Latest Anisian, Monte San Giorgio, Switzerland. Ischia and pubes, ventral view (approx. 2 cm long); *h*, *M. cornalius* (Bassani) after Repossi (1902). Middle Triassic Bituminous Shales, Besano, Italy. Reconstruction of pelvic girdle, dorsal view; *i*, *Mixosaurus* sp. UPMIZ EK-S/RMA 4-1976. Latest Anisian, Monte San Giorgio, Switzerland. Ischia and reduced pubes, ventral view (approx. 2.5 cm long).

loss of the obturator foramen (text-fig. 11*a, f, g*). Text-fig. 11*b-e* shows that the pelvic girdle was probably in articulation with the vertebral column in *Mixosaurus nordenskiöldii* from the earliest Anisian of Spitzbergen (Wiman 1923). *M. cornalianus* (Bassani) (text-fig. 11*h*) from near the Anisian/Ladinian boundary in Europe has an ilium which is less expanded proximally but still suggests the possibility of a similar connection.

In the Lower Liassic (text-fig. 12*a*) and later latipinnates, there is no connection between the girdle and the vertebral column and, in contrast with mixosaurs, the girdle bones are very small and quite different in shape. The ischium and pubis are fused in *Ophthalmosaurus* (text-fig. 12*b*) in which there is a thyroid fenestra (von Huene 1956, fig. 165).

TEXT-FIG. 12. Latipinnate pelvic bones. *a*, *Ichthyosaurus* sp., after Merriam (1908). Lower Liassic, Europe. Complete pelvic girdle; *b*, *Ophthalmosaurus* sp., after Andrews (1910). Oxford Clay, Peterborough. Ischio-pubes with thyroid fenestra.



Pelvic limb

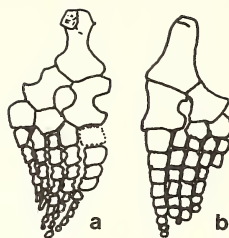
Mixosaur advances in the pelvic limb are shown most clearly in the proportions of the femur, the distal width being measured as a percentage of the length. Early Anisian mixosaurs have a mean of 68.66% while later Anisian/Ladinian forms show an increase in the relative distal width at 71.69% (see Table 3 and text-fig. 5*c*).

TABLE 3. $X = \frac{\text{Distal width of femur}}{\text{Length of femur}} \times 100$

	O.R.	\bar{X}	N	S	V
Early Anisian mixosaurs	64.61-72.22	68.66 \pm 56.53	2	6.29	9.16
Late Anisian/Ladinian mixosaurs	62.50-83.35	71.69 \pm 26.43	3	10.64	14.84
Lower Liassic latipinnates	49.80-78.37	63.42 \pm 6.73	8	8.05	12.69
Upper Jurassic latipinnates	32.47-69.38	58.57 \pm 10.94	7	11.83	20.19

Presumably this increase reflects the increase in breadth, at least proximally, of the mixosaur hind limb (text-fig. 13*a, b*). The Lower Jurassic and later latipinnates show an opposite but slower trend towards a relatively more slender femur supporting a narrow distal portion of the limb. The Lower Liassic mean is 63.42%, while that of the Upper Jurassic forms is 58.57% (Table 3).

Not only does the femur increase in breadth in mixosaurs, it also increases in length relative to the humeral length. The early Anisian value for femur length as a percentage of humerus length is 53.93%. The late Anisian/Ladinian mean is at the higher value of 55.35%. In Lower Liassic and later latipinnates the femur decreases in



TEXT-FIG. 13. Pelvic limbs of mixosauroids brought to the same femoral length. *a*, *Mixosaurus cornalianus* (Bassani), after Repossi (1902). Late Anisian, Besano; *b*, *M. nordenskiöldii* (Hulke), after Wiman (1910). Earliest Anisian, Spitzbergen.

length compared with the length of the humerus, the mean value being 75.72% for the lower forms and 60.96% for Upper Jurassic ophthalmosauroids (Table 4, text-fig. 5*d*).

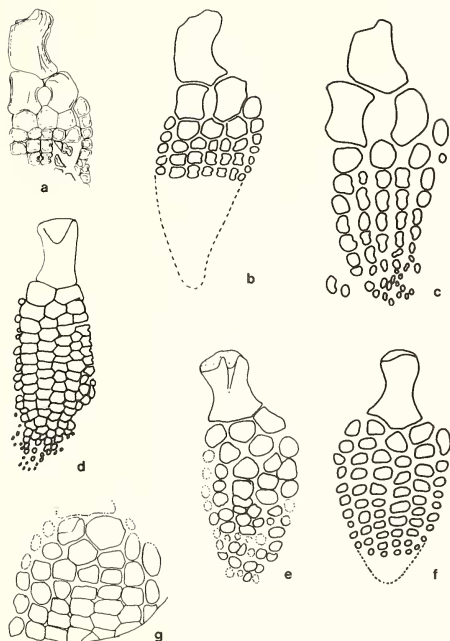
TABLE 4. $\bar{X} = \frac{\text{Femur length}}{\text{Humerus length}} \%$

	O.R.	\bar{X}	N	S	V
Early Anisian mixosauroid	53-93	53-93	1	—	—
Late Anisian/Ladinian mixosauroids	53.12-64.28	55.35 \pm 9.81	4	6.17	11.14
Lower Liassic latipinnates	60.00-88.88	75.72 \pm 8.83	8	10.56	13.94
Upper Jurassic latipinnates	57.74-63.42	60.96 \pm 1.90	7	2.05	3.37

DISCUSSION

The mixosauroids as a whole possess many primitive ichthyopterygian features such as the pentadactyl limb, the large pelvic girdle, the more elongate radius and ulna (text-fig. 14*a-c*), and tibia and fibula (text-fig. 13*a, b*), the shorter snout, the relatively small orbit in the earliest members, and the small pupil (Table 6). However, the advances described above indicate that all mixosauroids possessed a number of features which had already progressed further than those of their Lower Liassic and later counterparts. Such features include the exclusion of the lachrymal from the nasal opening by the maxilla, the more closed palate, and the structure of the vertebral column, especially caudally.

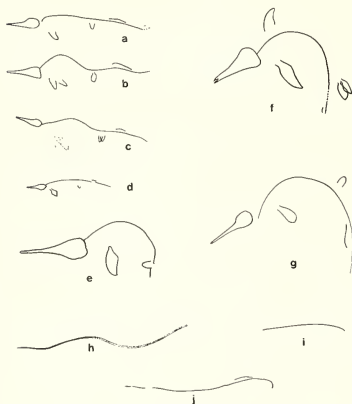
Here the different structures imply different functions in the two groups. In mixosauroids the high spines along the length of the vertebral column suggest relatively greater epaxial musculature than in Lower Liassic and later latipinnates, but the considerable rise in the caudal neural spines merits special consideration. Wiman (1910), in describing *M. nordenskiöldii* from the earliest Anisian of Spitzbergen, supposed that the higher neural spines just posterior to the pelvic girdle supported a caudal fin at a point where the vertebral column was slightly arched. His restoration showed a tail that drooped towards the tip. After criticizing the relative position of the high neural spines and the pelvic girdle in Wiman's specimen, Merriam (1911) reasserted that the high neural spines of the mixosauroids formed a primitive antecedent to the typical ichthyosauroid reversed heterocercal tail, and stated that this was 'possibly accompanied by a slight droop of the extreme posterior region'. Wiman (1916) defended his original description of *M. nordenskiöldii* and suggested that the



TEXT-FIG. 14. Pectoral fore limbs of mixosauroids and latipinnates brought to approximately the same humeral length (*g* is brought to the same humeral breadth as *e* and *f*). *a*, *Mixosaurus nordenskiöldii* (Hulke), after Wiman (1910). Early Anisian, Spitzbergen; *b*, *M. atavus* (Quenstedt), after von Huene (1916). Early Anisian, Germany; *c*, *M. cornalianus* (Bassani), after McGowan (1972). Late Anisian, Tre Fontane, Switzerland; *d*, *Ichthyosaurus intermedius* Conybeare, after Lydekker (1889). Lower Liassic, Street, Somerset; *e*, *Ophthalmosaurus* sp., after Appleby (1958). Oxford Clay, Peterborough; *f*, *Brachypterygius extremus* (Boulenger), after Boulenger (1904). Kimmeridge Clay, Dorset; *g*, *Myobradipterygius hauthali* von Huene, after von Huene (1925, 1956). Neocomian, Patagonia.

caudal fin was a dorsal fin which had moved back through the condition seen in *M. cornalianus* (Merriam 1908), until it had reached the tip of the tail by the beginning of the Jurassic, by which time the bend in the tail had become more pronounced and the high neural spines had disappeared. He particularly referred to the downward bend of the tail in Triassic mixosaurs as defining the position of the fin. Thus, early in the century the concept of a down-turned tail in the mixosaurs was introduced, emphasizing a similarity between mixosaurs and the Liassic and later forms.

However, schematic tracings of the vertebral column, limbs and skulls where possible, of one early Anisian and nine late Anisian/Ladinian forms (text-fig. 15),



TEXT-FIG. 15. Schematic diagrams of shapes of vertebral columns of mixosaurs. *a*, *Mixosaurus cornalianus* (Bassani), after Orlov (1964). Anisian; *b*, *Mixosaurus* sp. UPIMZ EK-S/RMA 6-1976. Late Anisian, Tessin, Switzerland; *c*, *Mixosaurus* sp. UPIMZ EK-S/RMA 4-1976. Late Anisian, Tessin, Switzerland; *d*, *M. cornalianus* (Bassani), after Dechaseaux (1955), picture reversed. Ladinian, Besano, Italy; *e*, *Mixosaurus* sp., traced from photograph of BMNH R. 5702. Anisian, Tre Fontane, Switzerland; *f*, *Mixosaurus* sp. UPIMZ EK-S/RMA 2-1976. Late Anisian, Tessin, Switzerland; *g*, *M. cornalianus* (Bassani), traced from a photograph of BMNH 8591 (cast of neotype). Middle Triassic, Besano, Italy; *h*, *Mixosaurus* sp., after Merriam (1908). Middle Triassic, almost certainly Italy; *i*, *Mixosaurus* sp., after Dechaseaux (1955). From a radiograph of the tail. Middle Triassic, Besano, Italy; *j*, *Mixosaurus* sp., traced from a photograph BMNH 5701. Middle Triassic, Edge Island, Spitzbergen.

show no preferred position for a tail-bend, although various curves in the vertebral column are present, many of them post-mortem effects. It therefore appears that the downward droop of the tail in Merriam's (1908) sketch and Wiman's (1910) restoration was no more than the drooped tail possessed by the majority of reptiles, and was not the precursor of the ichthyosaurian tail-bend. This latter did not exist in mixosaurs, although some kind of median fin-like shape would probably have been present in the anterior caudal position.

What, then, was the function of the high caudal spines? Similar structures occur in various positions along the vertebral column in many other groups of animals which do not possess a tail fluke. D'Arcy Thompson (1942) drew attention to the similarities between vertebral-column structures and the structures of bridges, pointing out that the compression members of certain bridges almost exactly recall the form of a backbone, while the tension members resemble the supra-spinous and nuchal ligaments which are connected to the neural spines. The high spines mentioned above suggest enlargement of the epaxial musculature in this region, as in the necks of horses and the tails of certain dinosaurs, used for raising the head and tail

respectively (Gregory, 1937). So, in addition to the sculling function of the tail suggested by the lateral position of the posteriormost rib facets and the compressed caudal centra, the mixosaur tail could be raised actively when necessary, but shows no downward flexibility to assist propulsion or diving.

In contrast to that of the mixosaurs, the tail of the Liassic and later latipinnates could not be raised to any significant degree, because the ball-and-socket joints of the anterior and posterior zygapophyses, the very low neural spines, and the approximation of the centra to each other, all limited dorsal movement on contraction of the epaxial musculature. The rib facets rising towards the tail-bend (text-figs. 8*d* and 9) suggest a progressive increase in the hypaxial over the epaxial musculature in the posterior caudal region, adding greater thrust in propulsion when contracted alternately, and enabling the angle of the tail-bend to be varied, especially when diving from the surface, when contracted together. This variation in angle may explain the weakness of the trend towards an increase in the angle of the tail-bend during ontogeny found by McGowan (1973*b*). Accounts of propulsion in ichthyosaurs have been given by Emichen (1938), Watson (1951), McGowan (1973*b*), and Robinson (1976).

Trends in other regions of the body support the exclusion of mixosaurs from latipinnate ancestry. The primitive nature of the pelvis in mixosaurs is in accordance with the structure and sculling function of the tail and the size of the hind limb. The latter increases in length and breadth throughout the Anisian and earliest Ladinian, suggesting its increasing importance in locomotion in this group. In Liassic and later latipinnates the reverse is the case, where a small and gradually diminishing girdle and hind limb reflect decreasing function.

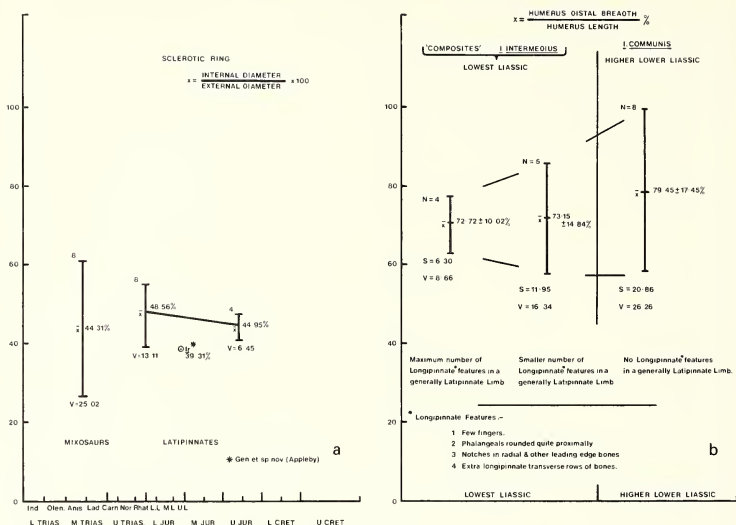
TABLE 5. $X = \frac{\text{Internal diameter of sclerotic ring}}{\text{External diameter of sclerotic ring}} \%$

	O.R.	\bar{X}	N	S	V
Early Anisian mixosaurs	—	—	—	—	—
Late Anisian mixosaurs	26.52-61.36	44.31 \pm 9.27	8	11.09	25.02
Lower Liassic latipinnates	38.64-55.55	48.56 \pm 5.32	8	6.36	13.11
Upper Liassic specimen	39.31	39.31	1	—	—
Upper Jurassic latipinnates	40.90-47.05	44.95 \pm 4.61	4	2.90	6.45

The fore limbs of both the mixosaurs and the Liassic and later latipinnates increased in breadth during their separate histories e.g. *Ophthalmosaurus* (text-fig. 14*e*), *Brachypterygius* (text-fig. 14*f*). Both groups depended to a greater or lesser extent on the fore limb for manoeuvrability, but the later mixosaurs from the Middle Triassic reached a more advanced stage than the first latipinnates from the earliest Liassic.

The same is true of the proportionate size of the orbit (text-fig. 5*a* and Table 1). The trends in both groups are of increase, but the later mixosaurs had reached a more advanced stage by the beginning of the Ladinian than had the first Liassic latipinnates, whose orbits increased gradually through the Jurassic until a maximum was reached in the ophthalmosaurids, which were very efficient divers (Watson 1951).

The size of the internal diameter of the sclerotic ring as a percentage of the external diameter falls in Jurassic latipinnates from 48.56% in the Lower Liassic to 44.95% in



TEXT-FIG. 16. *a*, quantitative comparisons of the sclerotic rings of late Anisian mixosaurs with Lower and Upper Jurassic latipinnates; *b*, bar diagrams of the distal breadth of the humerus expressed as a percentage of the length in 'composites' and *Ichthyosaurus intermedius*, both from the lowest Liassic, and *I. communis* from higher in the Lower Liassic.

the Upper Jurassic, while the latest mixosaurs have a mean value of 44.31%. This suggests an advance in the mixosaurs which behaved like most of the other measures considered above, changing at a more rapid rate than in the latipinnates, to become more advanced by the middle of the Middle Triassic than in the Lower Liassic latipinnates (text-fig. 16*a* and Table 5).

Finally, the difference in area of the internal sclerotic ring—presumed to reflect pupil size and hence light requirements—also agrees with these trends, the pupil remaining very small in mixosaurs, enlarged in the Lower Jurassic latipinnates, and of very great area in Upper Jurassic ophthalmosaurids (Table 6).

TABLE 6. X = Internal diameter of sclerotic ring (cm). The radius from which the internal area is calculated is taken as $\bar{X}/2$ (cm)

	O.R.	\bar{X}	N	S	V	$r = \bar{X}/2$ (cm)	πr^2 (sq. cm)
Early Anisian mixosaurs	—	—	—	—	—	—	—
Late Anisian/Ladinian mixosaurs	0.50-2.25	1.48 ± 0.19	6	0.83	34.13	0.74	1.72
Lower Liassic latipinnates	2.80-4.72	3.51 ± 0.48	8	0.57	16.37	1.75	9.68
Upper Liassic latipinnate	2.81	2.81	1	—	—	1.40	6.20
Upper Jurassic latipinnates	7.21-10.00	8.73 ± 2.49	4	1.35	15.53	4.36	59.88

Thus the mixosaurs must be removed from ancestry of the latipinnates, the general assemblage of characters described above, the different dentition and different diets (Kuhn-Schnyder 1964; Pollard 1968; Rieber 1970; and Keller 1976) suggesting an entirely different mode of life for the two groups, progressively diverging from the primitive through different periods of geological time.

Where, then, did the species of *Ichthyosaurus* s.s. originate? Either they descended from some unknown stock which has left no trace, or they originated in the only other group of ichthyosaurs extant at and before that time—the longipinnate ichthyosaurs.

THE 'COMPOSITE' FORMS

The fore limb of the 'composites' illustrated in text-figs. 1 and 2 show many gradations between longipinnates with a number of latipinnate features, to latipinnates with a number of longipinnate features. Skull measurements, where obtainable, support a taxonomic and evolutionary position between longipinnates and latipinnates. The more latipinnate-like members of the 'composites' and some specimens of *Leptopterygius tenuirostris* also have typically latipinnate coracoids (e.g. B. 1963' 27/O.S.) while other specimens of *L. tenuirostris* (B. 1963' 17/O.S.) and the longipinnate *Tenmodontosaurus platyodon* (von Huene 1922, pl. 13, fig. 31) have typically longipinnate coracoids. *L. tenuirostris* is thus an indivisible species intermediate between longipinnates and latipinnates.

It is suggested here that a major change took place—the separation of latipinnates from longipinnates. It seems that several different 'attempts' to achieve a latipinnate condition are represented in the 'composites' from the very early Liassic (pre-*planorbis* and *planorbis* Zones) for, though the fore limbs shown in text-fig. 2b (i), (ii) are certainly more latipinnate in the sense that an extra bone is present proximally, the bone is so proximal that it resembles neither typical latipinnates (text-fig. 1a) nor longipinnates (text-fig. 2d). No other specimen with this structure is known, but the remainder of the latipinnate-like 'composites' are similar to one another and are too numerous and stratigraphically restricted to be dismissed as species variation. All are from the very lowest beds of the Liassic of Britain, Germany, and France, e.g. the pre-*planorbis* and *planorbis* Zones of Street (Somerset), Keynsham (Avon), Barrow-on-Soar (Leicestershire), Newark (Nottinghamshire), the Lias α of Wurttemberg, Germany, and Ars, near Metz, France. The closest species morphologically to the latipinnate-like 'composites' is the one generally referred to as *Ichthyosaurus intermedius* Conybeare (text-fig. 14d), usually found in the same beds as the 'composites', although some have been found at the higher horizons in the Lower Liassic where *I. communis* Conybeare predominates and 'composites' of latipinnate aspect are absent.

I. communis and *I. intermedius* have been separated in the past, but McGowan (1969, 1974), using only the ratio of head to body length on six specimens from Street and six from Lyme Regis, and disregarding von Huene's (1922) other criteria, reduces the two species to sub-specific level. However, the coefficient of variability *V* (Simpson, Roe, and Lewontin 1960) for the group of twelve is abnormally high at 63.85 (Table 7) showing that this conclusion is probably invalid. This is further

supported by the fact that the majority of *I. intermedius* from the pre-*planorbis* and *planorbis* Zones is larger in size than *I. communis* from the *Schlotheimia angulata* to *Arnioceras semicostatus* Zones of Lyme Regis, even though their digital structure suggests that *I. communis* was more advanced. This is against the usual trend of size increase seen in all other ichthyosaur lineages.

TABLE 7. X = Length of body of McGowan's (1974) specimens

O.R.	\bar{X}	N	S	V
44-240	109.5	12	69.92 \pm 39.97	63.85

A study of the distal breadth of the humerus as a percentage of its length in *I. communis*, *I. intermedius*, and the 'composites' also shows that *I. intermedius* is closer to the 'composites' than to *I. communis* (Table 8 and text-fig. 16b). The longipinnate features, e.g. fewer fingers, less finger-splitting, phalangeals rounded more proximally, notches in the radials and other leading edge bones, and the extra longipinnate transverse rows of carpals, all present in the 'composites', occur in part in *I. intermedius* and are absent in *I. communis*, while the increasing values of V and S (standard deviation) indicate an increasing spread of the humeral ratio which accompanies the declining qualitative features mentioned above.

TABLE 8

$X = \frac{\text{distal width of humerus}}{\text{length of humerus}} \%$ for 'composites' of latipinnate aspects, *I. intermedius* and *I. communis*

	O.R.	\bar{X}	N	S	V
'composites'	64.22-78.36	72.72 \pm 10.02	4	6.30	8.66
<i>I. intermedius</i>	58.67-86.29	73.15 \pm 14.84	5	11.95	16.34
<i>I. communis</i>	59.13-100.00	79.45 \pm 17.45	8	20.86	26.26

CONCLUSIONS

It is likely that, in early Hettangian or Rhaetian times (von Huene 1922), one or more longipinnate stocks gave rise to a range of species (some longipinnate-like, others latipinnate-like) from which the earliest true latipinnates had their origins (text-fig. 17).

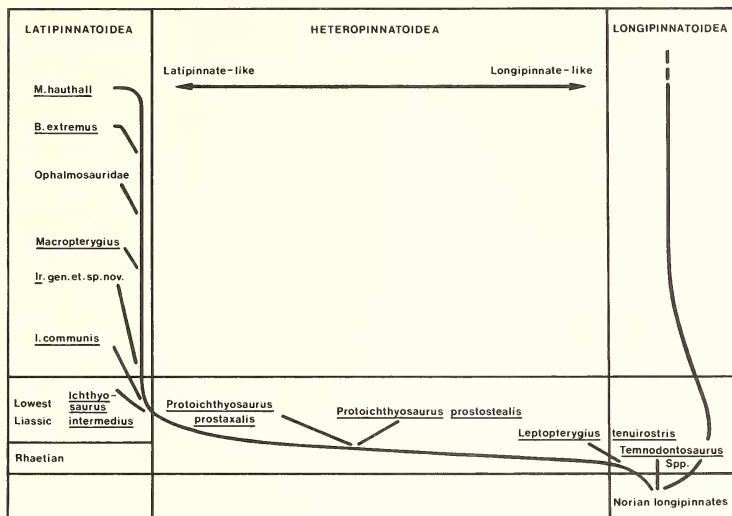
SYSTEMATIC DESCRIPTIONS

Class REPTILIA

Sub-Class ICHTHYOPTERYGIA

Order LONGIPINNATOIDEA von Huene, 1956, emend. nov.

Emended diagnosis. Ichthyopterygia with three distal carpals in fore limb. Nasal opening primitive or advanced in Triassic and Liassic members. Orbits small or large in Triassic and Liassic members. Ratio of distance between tip of snout and anterior tip of maxilla to length of jaw relatively small in Lower Liassic, rising in Upper Liassic (McGowan, 1972). Interclavicle T-shaped. Coracoid without or with very slight posterior notch. Glenoid anteriorly placed. Neural spines without caudal rise. Rib facets rise caudally to maximum dorsal position at tail-bend. Tail with vertical flukes. Pelvic elements separate or with fused ischio-pubis; abbreviated in Jurassic forms; no pubic foramen except in earliest members. Hind limb relatively long compared with fore limb. Range: Middle Triassic to Cretaceous.



TEXT-FIG. 17. Dendrogram showing probable evolutionary relationships between latipinnates (left), 'composites' (centre), and longipinnates (right).

Order LATIPINNATOIDEA von Huene, 1948, emend. nov.

Emended diagnosis. Ichthyopterygia with four distal carpals in fore limb. Nasal opening primitive (lachrymal takes part in boundary). Orbits larger than those of longipinnatoids in Lower Jurassic and very large in majority of Upper Jurassic forms. Ratio of distance between tip of snout and anterior tip of maxilla to length of jaw relatively large in Lower Jurassic (McGowan 1972), with exception of aberrant *I. breviceps*. Interclavicle T-shaped. Coracoid with well-developed posterior notch in most species. Glenoid anteriorly placed. Neural spines without caudal rise. Rib facets rise caudally to maximum dorsal position at tail-bend. Tail with vertical flukes. Pelvic elements separate but abbreviated in Lower Liassic. Ischiopubis in some Upper Jurassic forms. No pubic foramen. Hind limb relatively short compared with fore limb. Range: Lower Jurassic to Cretaceous.

Order HETEROPINNATOIDEA Ord. nov.

Diagnosis. Ichthyopterygia with at least one fore limb with a fourth primary digit originating (1) on the radial side from a row of three distal carpals, (2) on the radial side from a carpus comprising a row of four distal carpals plus a supernumary bone more proximally placed, and (3) on the ulnar side from four distal carpals. (1) and (2) are latipinnatoid-like, (3) is longipinnatoid-like. Nasal opening primitive (lachrymal takes part in boundary). Orbit at small end of longipinnate values given by McGowan (1972). Ratio of distance between tip of snout and anterior tip of maxilla to length of jaw intermediate between longipinnatoids and latipinnatoids in (1) and (2). Ratio large in (3). Interclavicle T-shaped. Coracoid with well-developed posterior notch in (1) and (2). Coracoid with all gradations between longipinnatoids and latipinnatoids in (3). Glenoid anteriorly placed. Neural spines without caudal rise.

Rib facets rise caudally to maximum dorsal position at tail-bend. Tail with vertical flukes. Pelvic elements separate, but abbreviated. No pubic foramen. Hind limb relatively short in (1) and (2) and relatively long in (3). Range: Lower Liassic.

Family PROTOICHTHYOSAURIDAE fam. nov.

Diagnosis. Latipinnatoid-like Heteropinnatoidea in which (1) at least one digit arises on the radial side of the three carpals, or (2) there is a carpus possessing the supernumary bone as described above.

Type genus: *Protoichthysaurus* gen. nov. Range: Hettangian up to and including the Zone of *Psiloceras planorbis*.

Genus *Protoichthysaurus* gen. nov.

Diagnosis. As for family. Type species *Protoichthysaurus prostaialis* sp. nov.

Protoichthysaurus prostaialis sp. nov.

Holotype. B. 1963'5/O.S. Lower Liassic, Moore Collection, Bath City Museum and Library.

Diagnosis. A member of the genus *Protoichthysaurus* in which all individuals of the species have a left or right limb with three distal carpals. In some individuals the opposite limb is in almost the same condition (text-fig. 1*b* (ii), bone X). Finger-splitting in phalanges on radial side of limb. The limbs with least finger-splitting have more notches on leading edge ossicles (e.g. text-fig. 1*e*). One or two ulnar sesamoids. Skull latipinnate-like but orbits smaller than in longipinnatoids. Ratio of distance between tip of snout and anterior tip of maxilla to length of jaw intermediate between latipinnatoids and longipinnatoids. Limbs and girdles of latipinnatoid aspect but with considerable variation of the distal end of the stem of the interclavicle. Humeri similar to *Ichthysaurus intermedius* in proportion of distal breadth to length, but with smaller range of variation.

Paratypes. B. 1963'7/O.S. Moore Collection. Almost certainly Lower Liassic, Street, Somerset; OUM J. 13,799. Duke of Marlborough's Collection. Lower Liassic, Street, Somerset; B. 1963'15/O.S. Moore Collection. Almost certainly Lower Liassic, Street, Somerset; LM 454'1951/164. Faulkes Collection. Lower Liassic, *planorbis* beds or earlier Hettangian, Barrow-on-Soar, Leicestershire.

Protoichthysaurus prosostealis sp. nov.

Holotype. B. 1963'24/O.S. Lower Liassic, Moore Collection, Bath City Museum and Library.

Diagnosis. Both fore limbs with supernumary bone surrounded by the radiale, radius, ulna, ulnare, intermedium and, in the left limb only, by a very small interval of the second of the four distal carpals.

Only one well-preserved specimen is known. Symmetry of the two fore limbs almost perfect; strong agreement between shapes of left and right supernumary bones. Interclavicle slightly longer than in *Protoichthysaurus prostaialis* and with non-bifurcate stem. Skull, girdle, limbs, and most of the remainder of the skeleton seen in ventral view and similar to *P. prostaialis*. Tip of skull missing. The triradiate pelvis and proximal ends of hind limbs preserved.

Measurements of humeri (cm)

	Left	Right
Length	10.95	9.50
Proximal width	6.40	6.00
Minimum breadth at neck	5.00	5.00
Distal breadth	7.00	7.05

Finger-splitting occurs on radial side and in the better preserved left limb, fusion of the split first digit occurs two rows distal to the split. The third ossicle in leading edge of hind limb notched.

Family LEPTOPTERYGIIDAE fam. nov.

Diagnosis. As for the single genus in this Family.

Type genus. *Leptopterygius* von Huene, 1922.

Genus *Leptopterygius* von Huene, 1922

Diagnosis. As for the single species in this genus.

Type species. *Leptopterygius tenuirostris* (Conybeare).

Leptopterygius tenuirostris (Conybeare 1822)

Holotype. A tooth figured in Conybeare (1822, p. 15, fig. 10). Now lost (Delair 1960, p. 70).

Neotype. IGS 51236 (McGowan 1974).

Emended diagnosis. As set out by McGowan (1974, p. 25) with the additional facts that the number of primary fingers may be three or four and that the coracoid shows all gradations in the species from longipinnatoid to latipinnatoid.

Remarks. McGowan (1974) placed this species in the latipinnates under the genus *Ichthyosaurus*. It has been regarded by all other authors as longipinnate since longipinnates and latipinnates were first recognized (e.g. Lydekker 1889; von Huene 1922, 1948, 1956; Appleby 1961; Romer 1966). This apparently strong difference of opinion arises from the incompleteness of the material in most collections, as stated by McGowan (1974). However, specimens such as B. 1963'27/O.S. from the Lower Liassic of Street have an essentially three-fingered fore limb with an accessory ulnar sesamoid finger as well as a latipinnate-like coracoid. Every gradation from longipinnates to latipinnates in McGowan's (1974) sense are known within this species. The numerical part of McGowan's (1974) emended diagnosis indicates its position intermediate between latipinnates and longipinnates, as set out by McGowan (1972). The problem of the taxonomic position remains but, at present, it seems best on general evolutionary grounds to place *L. tenuirostris* in its own family of the Heteropinnatoidea, because it represents another evolutionary trend away from the three-fingered longipinnates towards the latipinnate condition. The rank of family is used because the pattern of finger increase in *L. tenuirostris*, when it occurs, is quite different from that of the species of *Protoichthyosaurus*, for in *Leptopterygius* the fourth finger appears on the ulnar side of the limb. Notching is present in the radius and there is a tendency for the radius, ulna, and humerus to fuse. Delair (1974) has described an extreme case believing it to be an abnormality but varying degrees of fusion are often seen (Lydekker 1889). The radius and ulna frequently fuse round the foramen which usually exists between them.

There are thus two underlying patterns within the Heteropinnatoidea, one of which is latipinnate-like and contains two species, the other longipinnate-like. The differences between these two groups are considered to be greater than those between the families Ichthyosauridae and Ophthalmosauridae which are both latipinnatoid. The two heteropinnatoid groups are therefore considered to be of family rank.

Order MIXOSAUROIDEA Ord. nov.

Diagnosis. Ichthyopterygia with five distal carpals in fore limb. Nasal opening advanced by interposition of dorsal process of maxilla between lachrymal and nasal opening. Orbits of late Anisian/early Ladinian forms more advanced in diameter than any Lower Liassic ichthyosaur; small in early forms. Ratio of distance between tip of snout and anterior tip of maxilla to length of jaw intermediate between longipinnatoid and latipinnatoid conditions. Interclavicle never T-shaped. Coracoid with broad but shallow emargination. Glenoid posteriorly placed. Neural spines twice the height of the centrum; three times the height of the centrum at the caudal rise. Rib facets remain low on centra. No tail-bend, but tail laterally compressed. Pelvic elements separate but expanded. Pubic foramen present in early species only. Hind limb relatively long compared with fore limb, increasing through Anisian to beginning of Ladinian. Range: Earliest Anisian to earliest Ladinian. Only one Family known.

Family MIXOSAURIDAE Baur 1887, emend. von Huene, 1956

Type genus. *Mixosaurus* Baur.

Genus *Mixosaurus* Baur 1887, emend von Huene 1956, emend. nov.

Emended diagnosis. As set out by von Huene (1956) except that the pubis may or may not have a foramen.

Mixosaurus is the only known genus of mixosaurid; it contains six known species.

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REFERENCES

- ANDREWS, C. W. 1910. *The marine reptiles of the Oxford Clay*. London. B.M.(N.H.).
- APPLEBY, R. M. 1956. The osteology and taxonomy of the fossil reptile *Ophthalmosaurus*. *Proc. zool. Soc. Lond.* **126**, 403-447.
- 1958. *Ophthalmosauridae in the collections of the Leicester and Peterborough Museums*. Leicester Museums and Art Gallery. 1-47.
- 1961. On the cranial morphology of the ichthyosaurs. *Proc. zool. Soc. Lond.* **137**, 333-370.
- 1967. Sub-Class Ichthyopterygia in HARLAND, W. B. *et al.* (eds.), *The Fossil Record*. London (Geological Society), 696-697 and 699.
- and JONES, G. L. 1976. The Analogue Video Reshaper—a new tool for palaeontologists. *Palaeontology*, **19**, 565-586.
- BASSANI, F. 1886. Sui fossili e sull'età schisti bituminosi triasici di Besano in Lombardia. *Atti. Soc. Ital. Sci. Nat.* **29**, 15-66.
- BAUR, G. 1887. On the morphology and origin of the Ichthyopterygia. *Amer. Nat.* **21**, 837-840.
- BOULENGER, G. A. 1900. Osteologische Notizen über Ichthyosaurier. *Anat. Anz.* **18**, 574-588.
- BUCHAN, S. H., CHALLINOR, A. *et al.* 1965. The Triassic stratigraphy of Svalbard. *Norsk. Polarinstitutt Skriftr.*, no. 135, Oslo. 1-94.
- CONYBEARE, W. D. and DE LA BECHE, H. 1822. Notice of the discovery of a new fossil animal forming a link between the *Ichthyosaurus* and the crocodile. *Trans. geol. Soc. Lond.* **5**, 559-594.
- DECHASEAUX, C. 1955. *Ichthyopterygia* in PIVETEAU, J. *Traité de Paléontologie*, **5**: *Amphibiens, Reptiles, Oiseaux*. Paris: Masson et Cie.
- DELAIR, J. B. 1960. The Mesozoic reptiles of Dorset (Pt. III: Conclusion). *Proc. Dorset nat. Hist. archaeol. Soc.* **81**, 59-85.

- DELAIR, J. B. 1974. Two deformed ichthyosaur fore limbs from the English Lower Lias. *Mercian Geologist*, **5**, 101–103.
- DUNNINGTON, H. V., WETZEL, R. and MORTON, D. M. in DUBERTRET, L. 1959. Lexique stratigraphique international: Asie. (Congrès géologique international—Commission de Stratigraphie). Centre National de la Recherche Scientifique: Paris, **10**, 1–333.
- EDINGER, T. 1934. Ein *Mixosaurus*-Schädelrest aus Rüdersdorf. *Jahrb. preuss. geol. Landesanst.* **55**, 1–341.
- FRAAS, E. 1891. *Die Ichthyosaurier der sud-deutschen Trias-und Jura-ablagerungen*. Tübingen: Verlag Laupp.
- GILMORE, C. W. 1905. The osteology of *Baptanodon*. *Mem. Carneg. Mus.* **16**, 17–129.
- GREGORY, C. W. 1937. The bridge-that-walks. *Natural History*, **39**, 33–48.
- HUENE, F. VON 1916. Beiträge zur Kenntnis der Ichthyosaurier in deutschen Muschelkalk. *Palaeontographica*, **62**, 1–68.
- 1922. *Die Ichthyosaurier des Lias und ihre Zusammenhänge*. Berlin: Verlag von gebrüder Borntraeger. 114 pp., 22 pls.
- 1925. Einige Beobachtungen an *Mixosaurus cornalianus* (Bassani). *Zbl. Min. Geol. Paläont.* **B**, 1925, 289–295.
- 1948. Short review of the lower tetrapods in DU TOIT (ed.), Robert Broom Commemorative Volume. Royal Society of South Africa special publication. Capetown. Roy. Soc. S. Af.
- 1949. Ein Schädel von *Mixosaurus* und die Verwandtschaft der Ichthyosaurier. *Neues Jb. Geol. Paläont. Mh.* **B**, 1949, 88–95.
- 1956. *Palaeontologie und Phylogenie der niederen Tetrapoden*. Jena: Gustav Fischer Verlag.
- HULKE, J. W. 1873. Memorandum on some fossil vertebrate remains collected by the Swedish expeditions to Spitzbergen in 1864 and 1868. *Bihang. k. Svensk. Vet.-Akad. Handl.* **1**, 1–11.
- KELLER, T. 1976. Magen- und Darminhalte von Ichthyosauriern des süddeutschen Posidonienschiefers. *N. Jb. Geol. Paläont. Mh.* **5**, 266–283.
- KIPRIJANOFF, V. 1881. Studien über die fossilen Reptilien Russlands. T. I. Gattung *Ichthyosaurus* König aus dem Sewerischen Sandstein order Osteolith der Kreide-Gruppe. *Zap. Imp. Akad. Nauk.* **28**, 1–103.
- KUHN-SCHNYDER, E. 1964. Die Wirbeltierfauna der Trias der Tessiner Kalkalpen. *Geol. Rundschau*, **53**, 393–412. Stuttgart: Ferdinand Enke Verlag.
- LYDEKKER, R. 1889. *Catalogue of the fossil Reptilia in the British Museum (Nat. Hist.)*. London.
- MCGOWAN, C. 1969. The cranial morphology and interrelationships of the Lower Liassic ichthyosaurs. Ph.D. thesis, University of London. (Unpublished but available since late 1976.)
- 1972. The distinction between latipinnate and longipinnate ichthyosaurs. *Life Sciences occ. Papers, R. Ont. Mus.* **20**, 1–8.
- 1973a. The cranial morphology of the Lower Liassic latipinnate ichthyosaurs of England. *Bull. Br. Mus. nat. Hist. (Geol.)*, **24**, 1–109.
- 1973b. Differential growth in three ichthyosaurs: *Ichthyosaurus communis*, *I. breviceps* and *Stenopterygius quadricissus* (Reptilia Ichthyosauria). *Life Sci. Contr. R. Ont. Mus.* **93**, 1–24.
- 1974. A revision of the latipinnate ichthyosaurs of the Lower Jurassic of England (Reptilia, Ichthyosauria). *Life Sci. Contr. R. Ont. Mus.* **100**, 1–30.
- 1976. The description and phenetic relationships of a new ichthyosaur genus from the Upper Jurassic of England. *Can. J. earth Sci.* **13**, 668–683.
- MERRIAM, J. C. 1908. Triassic Ichthyosauria with special reference to the American forms. *Mem. Univ. Calif.* **1**, 1–196.
- 1910. Skull and dentition of a primitive ichthyosaurian from the Middle Triassic. *Univ. Calif. Publ., Bull. Dept. Geol.* **5**, 381–390.
- 1911. Notes on the relationships of the marine saurian fauna described from the Triassic of Spitzbergen by Wiman. *Univ. Calif. Publ., Bull. Dept. Geol.* **6**, 317–327.
- GEMICHEN, E. 1938. Essai sur la dynamique des ichthyosauriens *longipinnati* et particulièrement d'*Ichthyosaurus Burgundiae* (Gaud.). *Ann. Paléont.* **27**, 91–114.
- ORLOV, YU. A. 1964. *Osnovi Palaeontologii*. Moscow: Edit. 'NAUKA'. [In Russian.]
- PICKFORD, R. F. 1971. Charles Moore, 1815–1881 A brief history of the man and his geological collection. *Occ. Pap. Lib. and Mus. Dept., City of Bath*, **2**, 1–16.

- PINNA, G. 1967. La collezione di rettili triassici di Besano (Varese) del Museo Civico di Storia Naturale di Milano. *Natura, Milan*, **58**, 177-192.
- POLLARD, J. E. 1968. The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset. *Palaeontology*, **11**, 376-388.
- QUENSTEDT, F. A. 1852. *Handbuch der Petrefactenkunde*, **1**, Verschiedene Auflagen, 126 pp., 6 pls.
- REPOSSI, E. 1902. Il Mixosauo degli strati triassica di Besano in Lombardia. *Atti. Soc. ital. Sc. nat.* **41**, 361-372.
- RIEBER, H. 1970. *Phragmoteuthis? ticinensis* n. sp., ein Coleoidea-Rest aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kt. Tessin, Schweiz). *Paläont. Z.* **44**, 32-40.
- ROBINSON, J. A. 1976. Biomechanik des Schwimmens aquatischer Reptilien. *Zbl. Geol. Paläont.* **2**, 286-288.
- ROMER, A. S. 1966. *Vertebrate Paleontology*. Chicago University Press, Chicago, 468 pp.
- 1968. An ichthyosaur skull from the Cretaceous of Wyoming. *Contr. Geol.* **7**, 27-41.
- SIMPSON, G. G. ROE, A. and LEWONTIN, R. C. 1960. *Quantitative Zoology*. New York: Harcourt Brace & Co.
- SOLLAS, W. J. 1916. The skull of *Ichthyosaurus*, studied in serial sections. *Phil. Trans. R. Soc. Lond.* **B**, **208**, 63-126.
- THOMPSON, D'ARCY W. 1942. *On growth and form*. Cambridge University Press.
- WATSON, D. M. S. 1951. *Paleontology and modern biology*. Newhaven: Yale Univ. Press.
- WELNHOFER, P. (ed.) 1958. *Encyclopaedia of Palaeoherpetology*. Stuttgart: Gustav Fischer Verlag.
- WIMAN, C. 1910. Ichthyosaurier aus der Trias Spitzbergens. *Bull. geol. Inst. Univ. Upsala*, **10**, 124-148.
- 1912. Über *Mixosaurus cornalianus* Bass. sp. *Bull. geol. Inst. Univ. Upsala*, **11**, 230-241.
- 1916. Notes on the marine Triassic reptile fauna of Spitzbergen. *Univ. Calif. Publ., Geol.* **10**, 63-73.
- 1923. Über den Beckengürtel der Triasichthyosaurier. *Palaeont. Z.* **5**, 272-276.
- YOUNG, C.-C. 1965. On a revised determination of a fossil reptile from Jenhui, Kweichow with a note on a new ichthyosaur probably from China. *Vertebr. palasiat.* **9**, 368-375. [In Chinese.]
- and DONG, ZHI-MING. 1972. On the aquatic reptiles of the Triassic in China. *Inst. vertebr. Pal. Palaeoanthropology, Acad. Sin. Mem.* **9**, 1-34. [In Chinese.]

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